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Systematic implications of pinna venation and pinna anatomy in Zamiaceae

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Abstract Pinna venation and pinna anatomy were examined in ten species of six genera of Zamiaceae (Cycadales), which represent all four tribes. Pinna venation consists of dichotomous parallel veins without a midrib. The vein endings connect to each other in different forms in *Dioon spinulosum*, *Encephalartos friderici-guilielmii* and *Macrozamia moorei*, while they are never connected and reach the pinna margin in *Lepidozamia peroffskyana*, *Ceratozamia mexicana* var. *robusta*, *C. hildae*, *Zamia muricata*, *Z. debilis*, *Z. furfuracea* and *Z. floridana*, and gradually fade out in *L. peroffskyana*, *C. mexicana* var. *robusta*, and *C. hildae*. In transverse section, pinna generally consists of an adaxial epidermis and an abaxial epidermis, hypodermal sclerenchyma and mesophyll which may be differentiated into distinct adaxial and abaxial palisade regions, or adaxial palisade only, or entirely spongy tissue. However, typical spongy parenchyma and transfusion tissue are absent from this family. Mucilage canals are opposite the vascular bundles in *D. spinulosum*, or alternate with vascular bundles in *E. friderici-guilielmii*, *L. peroffskyana* and *M. moorei*. Girder sclerenchyma is connected with the abaxial epidermis only in *C. mexicana* var. *robusta* and *C. hildae*, but with both adaxial and abaxial epidermis in *Z. muricata*, *Z. debilis*, *Z. furfuracea* and *Z. floridana*. Pinna venation and anatomy support Stevenson's classification of Zamiaceae into two subfamilies.

Key words pinna venation, pinna anatomy, Zamiaceae.

After Reichenbach (1837) established the family Zamiaceae based on the genera *Zamia* L. and *Encephalartos* Lehm., all the later published genera, such as *Bowenia* Hook. ex J. D. Hook. and *Stangeria* T. Moore, were included in this family. Subsequently, cycad systematics received no significant attention until the publication of Johnson's (1959) monograph of the Australian genera, in which a new classification of the Cycadales was proposed. Johnson recognized three families, Cycadaceae, Zamiaceae and a new family Stangeriaceae, and divided Zamiaceae into three tribes and eight genera: *Lepidozamia* Regel, *Macrozamia* Miq. and *Encephalartos* in tribe Encephalarteae, *Dioon* Lindley in tribe Diooneae and *Microcycas* (Miq.) A. DC., *Ceratozamia* Brongn., *Zamia* and *Bowenia* in tribe Zamieae. However, certain other relationships remained unresolved at the familial, tribal and generic levels; in particular the placement of *Bowenia* in the tribe Zamieae was still problematic (Crane, 1988). Stevenson (1981) realized that *Bowenia* shared few characters with Zamieae and hence recognized the monogeneric family, Boweniaceae. Stevenson (1992) proposed a classification system of Cycadales based on a cladistic analysis of fifty-two characters ranging

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from morphology to phytochemistry. His system of the cycads has been recognized by modern taxonomists (Chen, 1995). In his system, Zamiaceae was subdivided into two subfamilies, four tribes, four subtribes and eight genera (Table 2).

The purposes of this paper are to provide new data on pinna venation and pinna anatomy in the context of recent ideas on systematic relationships within Zamiaceae. Earlier studies on Zamiaceae have mainly focused on morphological description and classification, including the pinna epidermis (Chamberlain, 1913; Thomas & Bancroft, 1913; Greguss, 1957, 1958, 1961; Pant & Nautiyal, 1963; Pant, 1973; Dehgan et al., 1993). Comprehensive comparative data on pinna anatomy in Zamiaceae were hitherto not available, although there are a few earlier reports of limited aspects. Miquel (1839) gave a brief description of venation. Lamb (1923) reviewed previous studies of leaflet anatomy and investigated 26 species representing nine genera of Cycadaceae *sensu lato*, which contains three modern families of Cycadales, including Zamiaceae. Brashier (1968) described vascularization of some cycads, which include six species of Zamiaceae. Norstog and Nicholls (1997) described the leaflet structure of *Cycas revoluta* Thunb., *Zamia integrifolia* Aiton, *Chigua* DW Stev. sp. and *Stangeria* sp., which represent the three families of Cycadales. Prior to this investigation, Lamb's (1923) work was therefore hitherto the most comprehensive. He studied the leaflet anatomy of all the genera in the cycadales except for *Chigua* and *Lepidozamia*, of which *Chigua* was studied by Norstog and Nicholls (1997) and *Lepidozamia* was examined here. In this paper, we focus on some aspects that earlier authors did not include, such as characters of pinna venation and stomatal apparatus.

1 Material and Methods

Materials examined are presented in Table 1. Material of *Ceratozamia hildae* was collected from Shenzhen Fairy Lake Botanical Garden. All the other species were collected from South China Botanical Garden, the Chinese Academy of Sciences (SCBG). All materials were fixed in FAA and mid-portion of the leaflets was sectioned using a sliding microtome at 15 – 30 μm thickness, at least three similarly aged individuals being examined. Sections were stained with Ehrlich hematoxylin, then dehydrated in an alcohol series and mounted in glycerin jelly. Standard methods of chemical maceration were used for epidermal preparation and isolation of tracheids and fibres (Johansen, 1940; Stace, 1965). Material was washed in water, stained with hematoxylin-safranin or methyl

Table 1 Source of Material*

Taxon	Provenance*	Voucher
Dioon spinulosum Dyer ex Eichl	SCBG	J. P. Liao & Y. J. Tang 99011
Encephalartos friderici-guilielmii Lehm.	SCBG	J. P. Liao & Y. J. Tang 99012
Lepidozamia peroffskyana Regel	SCBG	J. P. Liao & Y. J. Tang 99016
Macrozamia moorei F. Muell.	SCBG	J. P. Liao & Y. J. Tang 99030
Ceratozamia mexicana Brongn. var. *robusta* (Miq.) Thiselton-Dyer	SCBG	J. P. Liao & Y. J. Tang 99031
C. hildae G. P. Landry & M. C. Wilson	Shenzhen, Guangdong, China	J. P. Liao & Y. J. Tang 99032
Zamia muricata Willd.	SCBG	Y. J. Tang & J. P. Liao 99061
Z. debilis L. f. ex Salisb.	SCBG	Y. J. Tang & J. P. Liao 99062
Z. furfuracea Ait.	SCBG	Y. J. Tang & J. P. Liao 99063
Z. floridana DC.	SCBG	Y. J. Tang & J. P. Liao 99064

* SCBG, South China Botanical Garden, the Chinese Academy of Sciences. All vouchers are preserved in the Laboratory of Plant Structure and Development, South China Institute of Botany, the Chinese Academy of Sciences.

green, dehydrated through an alcohol series, cleared with xylene and finally mounted in neutral balsam. Observations were made and photographs were taken using an Olympus Vanox microscope. The vouchers and slide specimens are preserved in the Laboratory of Plant Structure and Development, SCBG.

2 Results

2.1 Pinna venation

Pinna venation is dichotomous parallel without a midrib in all species of Zamiaceae examined. The vein produces dichotomous branches at the base of pinna and these branches extend axially. The vein endings connect with each other in *D. spinulosum*, *E. friderici-guilielmii* and *M. moorei*, but are never connected and reach the pinna margin in *L. peroffskyana*, *Ceratozamia mexicana* var. *robusta*, *C. hildae*, *Z. debilis*, *Z. muricata*, *Z. floridana* and *Z. furfuracea*. The course of the vein endings is diverse. *D. spinulosum* has 11 – 16 parallel veins, of which those at two lateral parts of the pinna extend directly toward the pinna margin and the endings of those in the middle are connected with one another and then to the tip of pinna (Fig. 1). *E. friderici-guilielmii* has about 23 – 33 parallel veins which reach the upper margin of pinna and connect with one another at their endings; the connected endings then extend to the tip of pinna (Fig. 2). In *M. moorei* (Fig. 3), six parallel veins connect to one another and then extend to the tip of pinna. There are 10 – 11 parallel veins in *L. peroffskyana* (Fig. 4) and approximately 25 in *C. mexicana* var. *robusta* and *C. hildae*; parallel veins in these species terminate at the margin. There are 23 – 25 parallel veins in *Z. muricata* (Fig. 5), 24 in *Z. debilis*, 13 – 14 in *Z. floridana* (Fig. 6) and 39 – 43 in *Z. furfuracea* (Fig. 7); their parallel veins extend straight to the margin.

2.2 Pinna anatomy

2.2.1 Epidermis The epidermis is one layer of cells thick and consists of cells that are oval or nearly circular in transverse section (Figs. 8 – 28). The stomata are actinocytic in all species examined and usually restricted to the abaxial epidermis, except for *M. moorei* with stomata on both adaxial and abaxial epidermises (Fig. 15). Stomata are sunken and composed of guard cells and subsidiary cells. There are six subsidiary cells in *D. spinulosum*, *L. peroffskyana* and *E. friderici-guilielmii*, 5 – 6(7) ones in *M. moorei*, 4 – 6 in *C. mexicana* var. *robusta*, *C. hildae*, *Z. furfuracea*, *Z. debilis* and *Z. muricata*. Subsidiary cells are partially overlapped by the encircling cells which are raised to form an encircling cell rim. The encircling cell rims are at the same level as other epidermal cells in *D. spinulosum*, *C. hildae*, *Z. muricata*, *Z. debilis*, *Z. furfuracea* and *Z. floridana* (Fig. 14), nearly flat in *L. peroffskyana* or elevated in *E. friderici-guilielmii*, *M. moorei* and *C. mexicana* var. *robusta* (Figs. 17, 20).

2.2.2 Hypodermal sclerenchymatous cells The hypodermis consists of 1 – 2 layers of sclerenchymatous cells. Hypodermal sclerenchymatous cells occur adaxially in *D. spinulosum*, *E. friderici-guilielmii*, *L. peroffskyana*, *M. moorei*, *Z. muricata* and *Z. furfuracea* (Figs. 8 – 13, 15, 16, 23, 27) and abaxially in *E. friderici-guilielmii* and *Lepidozamia peroffskyana*. In *D. spinulosum*, *M. moorei* and *C. mexicana* var. *robusta*, hypodermal cells are occasionally present beneath the abaxial epidermis (Figs. 8 – 13, 15, 16, 18, 19 – 28).

2.2.3 Mesophyll Generally mesophyll is composed of palisade and spongy parenchyma. Palisade parenchyma contains 1 – 2 layers of parenchymatous cells. Spongy parenchymatous cells with small intercellular spaces are narrow, isodiametric to conspicuously elongated, the length being three to five times the width in some species. The distribution and differentiation of palisade parenchyma

Figs. 1–7. Venation patterns at the top of pinna. **1.** *Dioon spinulosum*. **2.** *Encephalartos friderici-guilielmii*. **3.** *Macrozamia moorei*. **4.** *Lepidozamia peroffskyana*. **5.** *Zamia muricata*. **6.** *Z. floridana*. **7.** *Z. furfuracea*. Scale bars = 4000 μm in Figs. 1, 2, 4, 5, 7, 8000 μm in Fig. 3, and 2000 μm in Fig. 6. The arrows show the vein endings connecting with each other.

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Figs. 8–17. Cross-sectional views of pinnae. **8, 9.** *Dioon spinulosum*. **10, 11.** *Encephalartos friderici-guilielmii*. **12–14.** *Lepidozamia peroffskyana*. **15–17.** *Macrozamia moorei*. Figs. 8, 10, 12, 15 show the middle parts of pinnae in transverse section (TS). Figs. 9, 11, 13, 16 show shape of pinna margin in TS. Figs. 14, 17 show stomata on the abaxial epidermis. Scale bars = 50 μm in Figs. 14, 17 and 200 μm in all other figures.

Abbreviations: Abh, abaxial hypodermal sclerenchyma; Adh, adaxial hypodermal sclerenchyma; Gs, girder sclerenchyma; Mc, mucilage canals; Pa, Palisade; Sa, stomatal apparatus; Vb, vascular bundles.

are different among the species examined. It is differentiated beneath the adaxial and abaxial epidermises in *M. moorei*, or only beneath the adaxial epidermis in *D. spinulosum*, *E. friderici-guilielmii*, *L. peroffskyana*, *C. mexicana* var. *robusta* (Fig. 18), *C. hildae* (Fig. 21), *Z. furfuracea* (Fig. 27) and *Z. floridana* (Fig. 28), or undifferentiated in *Z. muricata* and *Z. debilis* (Figs. 23, 25). No so-called transfusion tissue or accessary transfusion tissue is present. Calcium oxalate crystals are present in most species examined.

2.2.4 Vascular bundles Pinnae have no midrib in all species of Zamiaceae examined, but have several to many parallel vascular bundles (veins), which are usually enclosed by a sheath of slightly thickened parenchymatous cells. A strand of fibrous cells, girder sclerenchyma, connects the vascular bundle with one or both epidermises. Girder sclerenchyma is connected with the abaxial epidermis in *C. mexicana* var. *robusta* (Fig. 18) and *C. hildae* (Fig. 21), and with both abaxial and adaxial epidermises in *Z. muricata*, *Z. debilis*, *Z. furfuracea* and *Z. floridana* (Figs. 23, 25, 27, 28). It is absent from *E. friderici-guilielmii*, *L. peroffskyana* and *M. moorei* (Figs. 10, 12, 15). A few fibrous cells are scattered in the mesophyll or vascular tissue region in *D. spinulosum*, *M. moorei*, *C. mexicana* var. *robusta* and *C. hildae*.

2.2.5 Mucilage canals Conspicuous mucilage canals exist in *D. spinulosum*, *E. friderici-guilielmii*, *L. peroffskyana* and *M. moorei*. These are adaxially opposite to vascular bundles in *D. spinulosum* but alternate with vascular bundles in *E. friderici-guilielmii*, *L. peroffskyana* and *M. moorei*. In *M. moorei* mucilage canals are present only near the pinna margin.

2.2.6 Pinna margin The pinna margin is rounded or tapering in shape. In some species, such as *D. spinulosum*, *C. mexicana* var. *robusta*, *C. hildae*, *Z. muricata*, *Z. debilis*, *Z. floridana*, the pinna margin is curved as a beak (Figs. 9, 19, 22, 24, 26), while in *E. friderici-guilielmii*, *L. peroffskyana*, *M. moorei* and *Z. furfuracea* the pinna margin is rounded (Figs. 10, 13, 16). Marginal sclerenchyma is usually 2 – 3(4) layered, but one-layered in *Z. muricata* or 1 – 2 layered in *M. moorei* and *C. hildae*.

3 Discussion

Stevenson (1992) subdivided Zamiaceae into two subfamilies, Encephalartoideae and Zamioideae (Table 2).

This classification was based on a detailed cladistic analysis of 52 characters, but few anatomical characters were used for subfamilial division. However, this investigation indicates that several characters of pinna venation and anatomy, such as the presence or absence of mucilage canals and girder sclerenchyma, and the differences of pinna venation patterns, are diagnostic at the subfamilial level in Zamiaceae. Distinct differences of mucilage canal and girder sclerenchyma support Stevenson's classification, as mucilage canals are present and girder sclerenchyma absent in the subfamily Encephalartoideae, while mucilage canals are absent and girder sclerenchyma present in Zamioideae. Pinna venation patterns are also different between the two subfamilies: vein endings are connected in Encephalartoideae but unconnected in Zamioideae, with the single exception of *L. peroffskyana* with unconnected endings in the subfamily Encephalartoideae. There are hitherto no venation data in *Macrozamia* to our knowledge.

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Figs. 18 – 28. Cross-sectional (TS) views of pinnae. **18 – 20.** *Ceratozamia mexicana* var. *robusta*. **21, 22.** *Ceratozamia hildae*. **23, 24.** *Zamia muricata*. **25, 26.** *Z. debilis*. **27.** *Z. furfuracea*. **28.** *Z. floridana*. Figs. 18, 21, 23, 25, 27, 28 show the middle parts of pinnae in TS. Figs. 19, 22, 24, 26 show the shape of the pinna margin in TS. Fig. 20 shows stoma in abaxial epidermis. Scale bars = 50 μm in Fig. 20, and 200 μm in all other figures.
The abbreviations are the same as in Figs. 8 – 17.

Table 2 Stevenson's （1992） classification of Zamiaceae， and species whose leaflet anatomy have been examined by different authors

	Species examined	Reference
Subfamily Encephalartoideae		
Tribe Diooneae		
Dioon Lindl.	* *D. spinulosum* Dyer ex Eichl.	Lamb， 1923
	D. edule Lindl.	Lamb， 1923
Tribe Encephalarteae		
Subtribe Encephalartinae		
Encephalartos Lehm.	* *E. friderici-guilielmii* Lehm.	
	E. villosus Lehm.	Lamb， 1923
	E. hildebrandtii A. Braun & C. D. Bouch	Lamb， 1923
	E. lehmanni Lehm.	Lamb， 1923
	E. altensteinii Lehm.	Lamb， 1923
	E. caffer Lehm.	Lamb， 1923
	E. cycadifolius Lehm.	Lamb， 1923
	E. brachyphllus Lehm. & De Vriese	Lamb， 1923
Subtribe Macrozamiinae		
Macrozamia Miq.	* *M. moorei* F. Muell.	Lamb， 1923
Lepidozamia Regel	* *L. peroffskyana* Regel	
Subfamily Zamioideae		
Tribe Ceratozamieae		
Ceratozamia Brongniart	* *C. hildae* G. P. Landry & M. C. Wilson	
	* *C. mexicana* var. *robusta* （Miq.） Thiselton-Dyer	
	C. longifolia Miq.	Lamb， 1923
	C. mexicana Brongn.	Lamb， 1923
Tribe Zamieae		
Subtribe Microcycadinae		
Microcycas De Candolle	*Microcycas* sp.	Lamb， 1923
Subtribe Zamiinae		
Zamia L.	* *Z. muricata* Willd.	
	* *Z. debilis* L. f. ex Salisb.	
	* *Z. furfuracea* Ait.	Lamb， 1923
	* *Z. floridana* DC.	Lamb， 1923
	Z. integrifolia L. f.	Lamb， 1923；Norstog & Nicholls， 1997
	Z. pumila L.	Lamb， 1923
	Z. ottonis Miq.	Lamb， 1923
	Z. portoricensis Urban.	Lamb， 1923
Chigua D. W. Stevenson	*Chigua* sp.	Norstog & Nicholls， 1997

Asterisks indicate species examined here.

Characters of pinna venation and anatomy in Zamiaceae were compared with those of the other two families of Cycadales （Xie et al.， 2002）. Based on a brief description of leaves in cycads， Poole （1923） considered that the Zamiaceae more closely resemble the ancestral group than do Cycadaceae， and therefore appear to be more primitive. Stevenson （1990） recognized the presence of a midrib in the pinna to be derived within the cycads， and further observed that“ primitive ”patterns are also exhibited in certain fossil seed-fern pinnae. Norstog and Nicholls （1997） compared the structure of pinna within the three cycad families and considered that the Zamiaceae have the most primitive pattern because the members of the family lack midribs and have several to many parallel veins of approximately equal rank （except in *Chigua*）. This conclusion is also supported by this investigation. The evolutionary trend of venation patterns in Zamiaceae is apparently from absence to presence of midrib， numerous to few veins and vein endings at pinna tip connected to unconnected.

The genus *Chigua*, the only genus of Zamiaceae with a midrib, represents a possible link in this respect with the other cycad families, Stangeriaceae and Cycadaceae, but more work is required to confirm this. The occurrence of stomata apparatuses and marginal sclerenchyma in all species examined may represent a synapomorphy for Zamiaceae, whereas the occurrence of mucilage canals and girder sclerenchyma may be autapomorphic at subfamilial level in Zamiaceae. The evolutionary polarity of other characters of pinna anatomy is more difficult to assess, and requires testing by cladistic analysis. For mucilage canals, there may be a trend towards reduction, while for girder sclerenchyma there may be a trend towards increase.

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泽米科植物羽片脉序和解剖学及其系统学意义

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摘要　研究了苏铁目泽米科 Zamiaceae 2 亚科的所有 4 族（Stevenson 系统，1992）共 10 种代表植物的羽片脉序及解剖学特征，结果显示泽米科羽片脉序为二歧分叉的平行脉，无中脉。小刺双子铁 *Dioon spinulosum*、大头非洲铁 *Encephalartos friderici-guilielmii* 和摩尔大泽米 *Macrozamia moorei* 等的平行脉末端以不同的形式互相连接，而鳞木铁 *Lepidozamia peroffskyana*、粗壮角果铁 *Ceratozamia mexicana* var. *robusta*、竹叶角果铁 *C. hildae*、佛州泽米 *Zamia floridana*、柔叶泽米 *Z. debilis*、鳞秕泽米 *Z. furfuracea* 和短尖泽米 *Z. muricata* 等的平行脉末端不连接而直达叶缘，其中鳞木铁、粗壮角果铁和竹叶角果铁的脉达叶缘后逐渐消失。羽片的横切面结构通常由表皮、下皮厚壁细胞和叶肉组成，表皮层包括上、下表皮各一层，叶肉可能同时分化出近上表面的栅栏组织和近下表面的栅栏组织，或仅有近上表面的栅栏组织分化，或无栅栏组织分化而完全为海绵组织。然而，泽米科没有典型的海绵组织和传输组织分化。小刺双子铁、大头非洲铁、鳞叶木铁和摩尔大泽米的羽片具有粘液道而无工字厚壁组织，在小刺双子铁中粘液道与维管束对生，在另 3 种中则与维管束轮生；但粗壮角果铁、竹叶角果铁、佛州泽米、柔叶泽米、鳞秕泽米和短尖泽米的羽片则具有工字厚壁组织而没有粘液道，其中粗壮角果铁和竹叶角果铁的羽片工字厚壁组织仅与上表皮相连，而佛州泽米、柔叶泽米、鳞秕泽米和短尖泽米的羽片工字厚壁组织与上、下表皮都相连。羽片脉序和解剖学特征支持 Stevenson 将泽米铁科分为两亚科的观点。

关键词　羽片脉序；羽片解剖学；泽米科